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Nanjinganthus is an angiosperm, isn't it?

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ABSTRACT

Nanjinganthus is an Early Jurassic angiosperm recognized based on the study of over 200 specimens. However, some other authors have misinterpreted these fossils. Here the authors try to remedy the problems, by pointing out the logical pitfalls in these publications and underscoring a long-used, workable criterion for early angiosperms. The paper explains the cons and pros of this criterion, hoping to bring palaeobotany and plant taxonomy back to a consistent and practical track. *Nanjinganthus* is an angiosperm.

The discovery of the Early Jurassic (>174 Ma) angiosperm *Nanjinganthus* (Fu Q et al., 2018) has triggered a heated debate among botanists (Sokoloff DD et al., 2019; Taylor DW and Li H, 2018; Bateman RM, 2020; Coiro M et al., 2019; Rümpler F and Theißen G, 2019). Based on lack of pentamery alone, Sokoloff DD et al. (2019) reached a conclusion that *Nanjinganthus* is not an angiosperm.

The authors have to agree with Sokoloff DD et al. (2019) on the following facts. (1) "Pentamery is an angiosperm-specific character." (2) "Stable pentamery and tricolpate pollen as features almost restricted to eudicots." (3) Herendeen PS et al.'s (2017) interpretation of *Monetianthus* is at odds with previous research (Friis EM et al., 2001, 2009, 2011), as pointed out previously (Wang X, 2017). (4) Perianth of *Nanjinganthus* may be "displaced during fossilization".

Although the above points are justified, Sokoloff DD et al.'s main conclusion is shaky due to the following obvious flaws in their argument. First, Sokoloff DD et al. (2019) confused themselves with the concepts "angiosperms" and "eudicots", and there are several different competing and conflicting proposed criteria for angiosperms. Given that eudicots are a subset of angiosperms, pentamery and tricolpate pollen grains are features "almost restricted to eudicots" (a subset of angiosperms), and a feature of a subset (eudicots) does not necessarily occur in the whole set (angiosperms), then a logical inference should be that "*Nanjinganthus* is not an eudicot". The conclusion "*Nanjinganthus* is not an angiosperm", based on lack of pentamery in *Nanjinganthus* alone, *per se* implies that Sokoloff DD et al. (2019) have ignored the difference between "angiosperms" and "eudicots". Requiring tricolpate pollen grains for early angiosperms (Herendeen PS et al., 2017) and "a closed (*sensu lato*) carpel combined with double fertilization leading to endosperm formation" for early angiosperms (Bateman RM, 2020) are equally unworkable, especially under the light of "floral structures in early divergent angiosperms are highly diverse and often lack definitive features" (Bateman RM et al., 2006) and a closed carpel was "difficult" to prove in fossils (Bateman RM, 2020). Herendeen PS et al. (2017), Sokoloff DD et al. (2019), and Bateman RM (2020) have criteria inconsistent among themselves for recognizing angiosperms, although Bateman RM himself is a coauthor of Sokoloff DD et al. (2019). Even

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though the authors of Friis EM et al. (2001, 2011) themselves are among those of Herendeen PS et al. (2017), the early angiosperm *Monetianthus* (Friis EM et al., 2001, 2009, 2011) does not have the "unique angiosperm features" required for angiosperms by Herendeen PS et al. (2017). Second, Sokoloff DD et al. (2019) and Bateman RM's (2020) criteria would rule out all accepted early angiosperm fossils, since both pentamery and double fertilization are lacking in all recognized early angiosperms, including *Archaefructus* (Sun G et al., 1998), *Monetianthus* (Friis EM et al., 2001, 2009), *Nothodichocarpum* (Han G et al., 2017), *Schmeissneria* (Wang X, 2010), *Hexagyne* (Coiffard C et al., 2014), among many. Third, Sokoloff DD et al. (2019) and Bateman RM's (2020) criteria are ruled out by extant angiosperms. Sokoloff DD et al.'s (2019) criterion is not applicable for more than 100000 species of extant angiosperms (including monocots and ANITA clades) that lack pentamery. Lack of double fertilization in Podostemaceae (angiosperms) requires Bateman RM (2020) to further fix his criterion for recognizing angiosperms, and Bateman RM (2020) did not mention the existence of double fertilization in gymnosperms (Friedman WE, 1992). In short, both Sokoloff DD et al.'s and Bateman RM 's criteria, although different each other, are equally inapplicable for angiosperms, living and fossil.

The sepals and petals in *Nanjinganthus* are all arranged along the upper margin of the inferior ovary, without obvious intervals in between (Fu Q et al., 2018). Given that a "whorled arrangement" in plants is frequently taken as "in a series with relatively short plastochrons " (Buzgo M et al., 2004) and that no consensus on perianth phyllotaxy in repeatedly-studied *Monetianthus* can be reached even among the same group of authors (Friis EM et al., 2001, 2009, 2011), the authors have no reason to object describing the perianth arrangement in *Nanjinganthus* as "whorled". Sokoloff DD et al.'s (2019) analysis was based on only 2 two-dimensional pictures of 2 of over 200 *Nanjinganthus* flowers that were not free of displacement and artifacts. Given that the authors, after observing over 200 three-dimensionally preserved flowers, cannot reach a definitive conclusion on perianth arrangement in *Nanjinganthus* (Fu Q et al., 2018), whether Sokoloff DD et al. (2019) could do it is apparently an open question.

The male or female cone-interpretations of *Nanjinganthus* by Sokoloff DD et al. (2019) and Coiro M et al. (2019) fall apart due to the obvious lack of a continuous cone axis running from the bottom to the tip of the organ in *Nanjinganthus*. The only "reason" of Coiro M et al. (2019), "obscure" morphology of the inferior ovary in *Nanjinganthus*, is the result of their ignoring the inferior ovary in Figs. 2e−f, h, j, 3a−b, 3f, 4c−d, 5f−h, 6a−b, 6f−l and 7a−b,7e−i of Fu Q et al. (2018).

Our criterion for fossil angiosperms is "ovule enclosed at or before the time of pollination" (Tomlinson PB and Takaso T, 2002; Fu Q et al., 2018; Wang X, 2018). Such a criterion is not perfect and has its own shortcoming (it excludes some angiosperms, although only a few, with ovules not physically fully enclosed), but its advantage is obvious: Once a plant meets this criterion, it is safe to say that the plant is an angiosperm. *Nanjinganthus* has met this criterion (Figs. 1a−e).

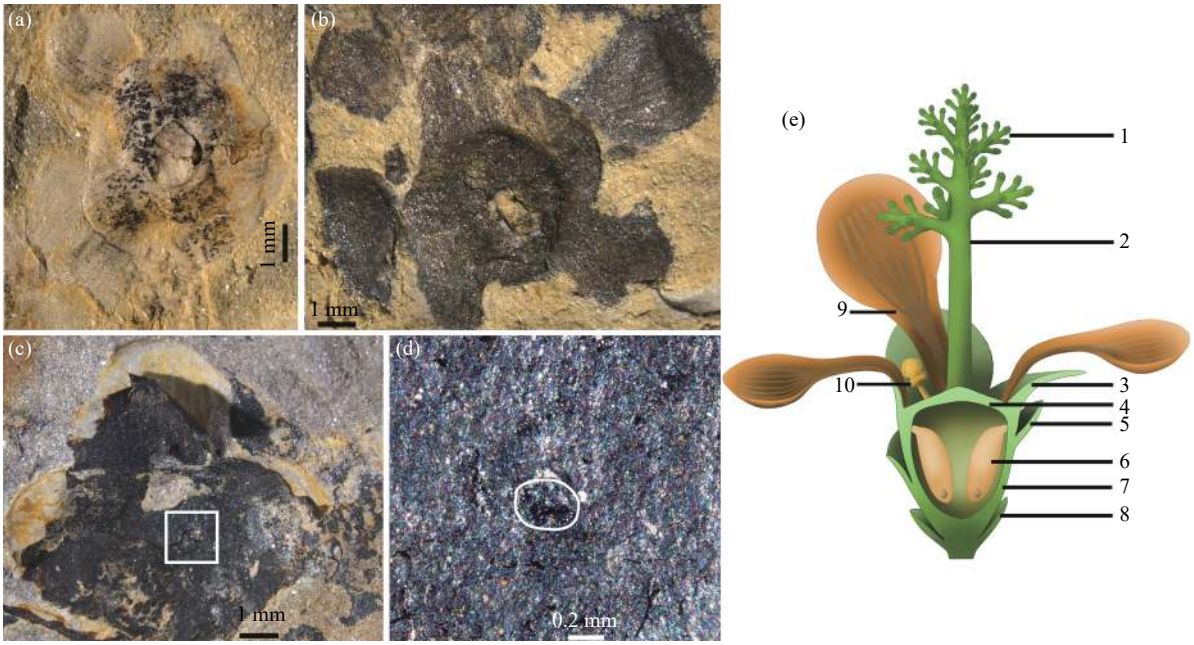

Fig. 1. Top views of *Nanjinganthus dendrostyla*, showing an ovary with ovarian roof removed and two seeds inside (a), another ovary with ovarian roof partially removed and only one seed visible (b), and a coalified flower with intact ovarian roof and no seeds visible (c). d−the intact integral ovarian roof of the flower in rectangle in c, with a style scar (white circle) on the top of the complete and intact ovarian roof. e−the reconstruction of *Nanjinganthus*. 1−branches of dendroid style; 2−dendroid style; 3−sepal; 4−ovarian roof; 5−scale; 6−seed; 7−cup-form receptacle/ovary; 8−bract; 9−petal; 10−unknown organ (staminode?). Scale bar = 1 mm in a, b, c, and scale bar = 0.2 mm in d. Reproduced from figures (Figs. 4c, 5h, 6f, 6l, 11) of Fu Q et al. (2018) published on eLife under the Creative Commons Attribution 4.0 International Public License (CC BY 4.0; https://creativecommons.org/licenses/by/4.0/).

In summary, although there is uncertainty about its perianth phyllotaxy, *Nanjinganthus* remains a *bona fide* angiosperm from the Early Jurassic. The doubt over *Nanjinganthus* by Sokoloff DD et al. (2019), Coiro M et al. (2019) and Bateman RM (2020) can be easily refuted.

CRediT authorship contribution statement

Qiang Fu, José B. Diez, Mike Pole, Manuel García-Ávila, and Xin Wang contributed to the analysis of results and references and to the writing of the manuscript.

Declaration of competing interest

The authors declare no conflict of interest.

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